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Weak effects of geolocators on small birds: A meta-analysis controlled for phylogeny and publication bias

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Abstract

1. Currently, the deployment of tracking devices is one of the most frequently used approaches to study movement ecology of birds. Recent miniaturization of light-level geolocators enabled studying small bird species whose migratory patterns were widely unknown. However, geolocators may reduce vital rates in tagged birds and may bias obtained movement data.
2. There is a need for a thorough assessment of the potential tag effects on small birds, as previous meta-analyses did not evaluate unpublished data and impact of multiple life-history traits, focused mainly on large species and the number of published studies tagging small birds has increased substantially.

3. We quantitatively reviewed 549 records extracted from 74 published and 48 unpublished studies on over 7,800 tagged and 17,800 control individuals to examine the effects of geolocator tagging on small bird species (body mass <100 g). We calculated the effect of tagging on apparent survival, condition, phenology and breeding performance and identified the most important predictors of the magnitude of effect sizes.
4. Even though the effects were not statistically significant in phylogenetically controlled models, we found a weak negative impact of geolocators on apparent survival. The negative effect on apparent survival was stronger with increasing relative load of the device and with geolocators attached using elastic harnesses. Moreover, tagging effects were stronger in smaller species.
5. In conclusion, we found a weak effect on apparent survival of tagged birds and managed to pinpoint key aspects and drivers of tagging effects. We provide recommendations for establishing matched control group for proper effect size assessment in future studies and outline various aspects of tagging that need further investigation. Finally, our results encourage further use of geolocators on small bird species but the ethical aspects and scientific benefits should always be considered.

KEYWORDS
condition, migration, phenology, reproduction, return rate, survival, tag effect, tracking device

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1 | INTRODUCTION

Tracking devices have brought undisputed insights into the ecology of birds. The use of these tags has enabled researchers to gather valuable information about the timing of life events across annual cycles, the year-round geographic distribution of populations and other important ecological patterns in many species whose movement ecology was widely unknown (e.g. Patchett, Finch, & Cresswell, 2018; Stanley, MacPherson, Fraser, McKinnon, & Stutchbury, 2012; Weimerskirch et al., 2002). A significant proportion of recently published tracking studies use light-level geolocators on small bird species (body mass up to 100 g; Bridge et al., 2013; McKinnon & Love, 2018); however, the increasing use of these tags on small birds raises questions about ethics of tagging and how representative the behaviour of tagged individuals is (Jewell, 2013; Wilson & McMahon, 2006).

Studies using tracking devices such as archival light-level geolocators (hereafter "geolocators") frequently report the effect of tagging. The published results on the effects of geolocator tagging are equivocal: Some found reduced apparent survival, breeding success and parental care (Arlt, Low, & Pärt, 2013; Pakanen, Rönkä, Thomson, & Koivula, 2015; Scandolara et al., 2014; Weiser et al., 2016) while others report no obvious effects (Bell, Harouchi, Hewson, & Burgess, 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk, Souchay, Jenni-Eiermann, Bauer, & Schaub, 2015). Recent meta-analyses evaluating the effects of geolocators (Costantini & Møller, 2013) and other tracking devices (Barron, Brawn, & Weatherhead, 2010; Bodey et al., 2018a) showed slightly negative effects on apparent survival, breeding success and parental care. These studies also discussed relative load as an aspect affecting the tagged birds (Costantini & Møller, 2013), or suggested multiple threshold values of relative load on birds (Barron et al., 2010; Bodey et al., 2018a). However, these studies involved mainly large bird species where the same additional relative load will more negatively affect surplus power and thus the flight performance than in smaller species (Caccamise & Hedin, 1985). Moreover, previous studies did not control for the effect of small-sample studies, or phylogenetic non-independence and its uncertainty. There is thus a lack of systematic and complex evaluation of geolocator effects on small birds including species' life-history and ecological traits, geolocator design, and type of attachment.

Almost all prior meta-analyses reporting effects of tagging relied only on published sources and could thus be affected by publication bias (Koricheva, Gurevitch, & Mengersen, 2013), as omitting unpublished sources in meta-analyses may obscure the result (see, e.g. Sánchez-Tójar et al., 2018). The main source of publication bias in movement ecology could be a lower probability of publishing studies based on a small sample size, including studies where no or only few tagged birds were successfully recovered due to a strong tagging effect. Additionally, geolocator effects most frequently rely on comparisons between tagged and control birds and a biased choice of control individuals may directly lead to the misestimation of the tagging effect sizes. The bias in the control groups can be due to selection of smaller birds, birds being caught in different spatiotemporal conditions, including non-territorial individuals, or different effort put into recapturing control and tagged individuals.

The number of studies tagging small birds is rapidly increasing each year even though our understanding of tag effects is incomplete. In this study, we evaluated the effects of tagging on apparent survival, condition, phenology and breeding performance for small bird species (<100 g) in a robust dataset of both published and unpublished studies to minimize the impact of publication bias. Moreover, we assess whether the tagging effects are related to species' ecological and life-history traits, type of control treatment as well as geolocator and attachment designs. We build on the most recent advances in meta-analytical statistical modelling to get unbiased estimates of the geolocator deployment effects controlled for phylogenetic non-independence and its uncertainty (Doncaster & Spake, 2018; Guillerme & Healy, 2017; Hadfield, 2010; Viechtbauer, 2010).

2 | PREDICTIONS

1. Geolocators will negatively affect apparent survival, condition, phenology and breeding performance of small birds.
2. Negative effects will be stronger in unpublished studies than in published studies.
3. Deleterious effects will be most prominent in studies establishing matched control groups compared to studies with potentially biased control groups.
4. Geolocators which constitute a higher relative load will imply stronger negative effects.
5. Geolocators with a longer light stalk/pipe will cause stronger negative effects because of increased drag in flight and thus increased energetic expenditure (Bowlin et al., 2010; Pennycuick, Fast, Ballerstädt, & Rattenborg, 2012). These effects will be stronger in aerial foragers than in other foraging guilds (Costantini & Møller, 2013).
6. Non-elastic harnesses will cause stronger negative effects than elastic harnesses, which better adjust to intra-annual body mass changes and avoid flight restriction (Blackburn et al., 2016).

3 | MATERIALS AND METHODS

3.1 | Data search

We conducted a comprehensive search for both published and unpublished studies deploying geolocators on bird species with body mass up to 100 g. We searched the Web of Science Core Collection (search terms: TS = (geoloc* AND (bird* OR avian OR migra*) OR geologg*)) and Scopus databases (search terms: TITLE-ABS-KEY (geoloc* AND (bird* OR migra*) OR geologg*)), to find published studies listed to 18 February 2018. Moreover, we searched reference lists of studies using geolocators on small birds and included studies from previous comparative studies (Bridge et al., 2013; Costantini & Møller, 2013; Weiser et al., 2016). In order to obtain information from unpublished studies, we inquired geolocator producers and the Migrant Landbird Study Group to disseminate our request for unpublished study details among their customers and members, respectively. In addition, we asked the corresponding authors of the published studies to share any unpublished data. The major geolocator producers—Biotrack, Lotek, Migrate Technology and the Swiss Ornithological Institute—sent our request to their customers. To find whether the originally unpublished studies were published over the course of this study, we inspected their status on 1 December 2018. The entire process of search and selection of studies and records (described below) is presented in a flow chart (Supporting Information Figure S1).

3.2 | Inclusion criteria; additional data requesting

We included studies that met the following criteria:

1. The study reported response variables (e.g. return rates, body masses) necessary for effect size calculation.
2. The study included a control group of birds alongside the geolocator-tagged individuals or reported a pairwise comparison of tagged birds during geolocator deployment and recovery.
3. As a control group, the study considered birds marked on the same site, of the same sex and age class without any indication of a difference in recapture effort between tagged and control groups.
4. For pairwise comparisons, the study presented correlation coefficients or raw data.
5. The variable of interest was presented outside the interaction with another variable.

In order to obtain robust and unbiased results, we asked the corresponding authors for missing data or clarification when the criteria were not met or when it was not clear whether the study complied with the criteria (70% response rate [n = 115]). In addition, we excluded birds that had lost geolocators before subsequent recapture as we did not know when the bird lost the geolocator, and excluded all individuals tagged repeatedly over years because of possible interannual carry-over effects of the devices. VBr assessed all studies for eligibility and extracted data; the final dataset was cross-checked by JK and PP. A list of all published studies included in the meta-analysis is provided in the Published Data Sources section.

3.3 | Trait categories; effect size calculation; explanatory variables

We divided all collected data into four trait categories: apparent survival, condition, phenology and breeding performance based on the response variables reported (e.g. interannual recapture rates, body mass changes, arrival dates or clutch sizes; Supporting Information Table S2). These categories represent the main traits possibly affected in the geolocator-tagged individuals. Subsequently, analyses were run separately for each trait category. We calculated the effect sizes for groups of tagged birds from the same study site and year of attachment, of the same sex (if applicable) and specific geolocator and attachment type accompanied with the corresponding control groups. For simplicity, we call these units *records* throughout the text. For each record, we extracted a contingency table with the treatment arm continuity correction (Schwarzer, Carpenter, & Rücker, 2014) or mean, variance, and sample size, to calculate the unbiased standardized mean difference—Hedges' g (Borenstein, Hedges, Higgins, & Rothstein, 2009)—and its variance with correction for the effect of small sample sizes (Doncaster & Spake, 2018). We used the equation from Sweeting, Sutton, and Lambert (2004) to calculate variance in pairwise comparisons. When raw data were not provided, we used the reported test statistics (F, t or χ^2) and sample sizes to calculate the effect size using the R package compute.es (Del Re, 2013). Besides the effect size measures, we extracted additional variables of potential interest—ecological and life-history traits per species, methodological aspects of the study, geolocator and attachment designs and harness material elasticity (Table 1).

3.4 | Accounting for dependency

We accounted for data non-independence on several levels. When multiple records shared one control group (e.g. several geolocator types and attachment designs used in one year), we split the sample size in the shared control group by the number of records to avoid a false increase in record precision. When multiple measures were available for the same individuals, we randomly chose one effect size measure in each trait category (n = 8). If the study provided both recapture and re-encounter rates, we chose the re-encounter rate as a more objective measure of apparent survival. Re-encounters included captures and observations of tagged birds, and thus, the bias towards the tagged birds caused by the potentially higher recapture effort to retrieve the geolocators should be lower. Finally, we accounted for phylogenetic non-independence between the species and the uncertainty of these relationships using 100 phylogenetic trees (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) downloaded from the BirdTree.org (www.birdtree.org) using the backbone of Hackett et al. (2008). Moreover, we used the random intercepts of species and study sites in all models, the latter to account for possible site-specific differences (such as different netting effort or other field methods used by particular research teams).

3.5 | Overall effect sizes and heterogeneity

We calculated the overall effect size for each trait category from all available records using meta-analytical null models. We employed the *MCMCglmm* function from the MCMCglmm package (Hadfield, 2010) to estimate overall effect sizes not controlled for phylogeny (model 1, Supporting Information Table S3). We then used the *mulTree* function from the mulTree package (Guillerme & Healy, 2017) to

TABLE 1 Explanatory variables used in the multivariate meta-analysis of apparent survival extracted from published and unpublished geolocator studies or from the literature. *N* presents the number of records specified as the groups of tagged birds from the same study site, year of attachment, of the same sex and the specific geolocator and the attachment type accompanied with the corresponding control groups

		Description	*N*
Methodological aspect			
	Published data	Published—data from published studies (for details see Methods), data from unpublished sources from years following an already published study or data initially collected as unpublished but published by 31 August 2018	303
		Unpublished—data from unpublished studies	123
	Control group	Matched—birds handled in the exactly same way as geolocator-tagged birds except for geolocator deployment	102
		Marked only—birds of the same sex, age, from the same year and study site or birds from the same site, from different years	324
Species trait			
	Foraging strategy[b,c]	Aerial forager	122
		Non-aerial forager	304
	Sex	Males	195
		Females	120
Geolocator specification			
	Relative load	% of geolocator mass (including the harness) of the body mass of the tagged birds	418
	Stalk/pipe length[a]	Length (mm) of the stalk/pipe holding the light sensor or guiding the light towards the sensor (0 mm for stalkless models)	371
Attachment specification			
	Attachment type	Leg-loop harness	304
		Full-body harness	80
		Leg-flag attachment	42
	Material elasticity[a]	Elastic—elastan, ethylene propylene, neoprene, rubber, silicone, silastic or Stretch Magic	235
		Non-elastic—cord, kevlar, nylon, plastic, polyester or teflon	146
Ecological trait			
	Life histories	Great circle distance between geolocator deployment site and population-specific centroid of the non-breeding (or breeding) range	426
		Male body mass (g)	426
		Female body mass (g)	426
		Nest type—open/close	426
		Clutch size (number of eggs)	426
		Number of broods per year	426
		Dense habitat preference (species occurs especially in dense habitats, e.g. reeds or scrub)—yes/no	426
		Egg mass (g)—mean fresh mass[d]	426
		Clutch mass (g)—egg mass × clutch size	426

[a]Only used for harness attachments. [b]Cramp & Perrins, 1977–1994. [c]Rodewald, 2015. [d]Schönwetter, 1960–1992.

automatically fit a MCMCglmm model on each phylogenetic tree and summarised the results from all these models to obtain phylogenetically controlled overall effect size estimates (model 2, Supporting Information Table S3). We used weakly informative inverse-Gamma priors (V = 1, nu = 0.002) in all models. All fitted MCMCglmm models converged and Gelman–Rubin statistic was always <1.1 for all parameters. As our data contained many effect sizes based on small sample sizes, which could lead to a biased estimate of the overall effect size variance, all effect sizes were weighted by their mean-adjusted sampling variance (Doncaster & Spake, 2018). We considered effect sizes (Hedge's *g*) of 0.2, 0.5 and 0.8 weak, moderate and large effects, respectively. Moreover, we calculated the amount of

TABLE 2 Number of unpublished effect sizes included in the analysis and Egger's regression tests of the null model residuals against their precision to assess the presence of publication bias

	Unpublished (%)		Egger's regression			
Trait category	**Effect sizes**	***N***	**Intercept**	***t***	***SE***	***p***
Apparent survival	28.9	426	0.12	1.53	0.08	0.121
Condition	63.3	79	−0.36	−1.70	0.21	0.088
Phenology	59.1	22	−0.26	−1.28	0.21	0.217
Breeding performance	27.3	22	−0.01	−0.01	0.61	0.993

between-study heterogeneity in all null models using the equation described in Nakagawa and Santos (2012). Phylogenetic heritability (H^2) expressing the phylogenetic signal was estimated as the ratio of phylogenetic variance ($\sigma^2_{\text{phylogeny}}$) against the sum of phylogenetic and species variance ($\sigma^2_{\text{species}}$) from the models (Supporting Information Table S3; Hadfield & Nakagawa, 2010):

$$H^2 = \sigma^2_{\text{phylogeny}} / (\sigma^2_{\text{phylogeny}} + \sigma^2_{\text{species}}).$$

3.6 | Multivariate meta-analysis

To unveil the most important dependencies of the geolocator effects, we calculated three types of multivariate models: a full trait model (model 3), an ecological model (model 4) and models of publication bias (model 5, Supporting Information Table S3). In the full trait model, we used methodological, species, geolocator specification and attachment variables (Table 1) to estimate their impact on apparent survival (model 3). We did not compare the tagging effects of different attachment types due to their use in specific groups of species (e.g. the leg-flagged attachment in shorebirds or the full-body harnesses in nightjars and swifts only). Prior to fitting the ecological model, we employed a principal component analysis of the intercorrelated log continuous life-history traits and extracted the two most important ordination axes—PC1 and PC2 (Table 1). The PC1 explained 54.4% of the variability and expressed a gradient of species characterized mainly by increasing body mass, egg mass and clutch mass (Supporting Information Figure S4). The PC2 explained 18.7% of variance and was characterized mainly by increasing clutch sizes, number of broods and decreasing migration distances (Supporting Information Figure S4). These axes together with the categorical ecological traits (Table 1) were then entered into the ecological model to estimate their effect on apparent survival (model 4). Finally, we tested for differences in effect sizes between published and unpublished results in each trait category using all available records (model 5). In these models, we employed the *rma.mv* function from the R package metafor (Viechtbauer, 2010) weighted by the mean-adjusted sampling error (Doncaster & Spake, 2018). Continuous predictors were scaled and centred. None of the model residuals violated the assumptions of normal distribution. Because the phylogenetic relatedness of the species explained only a small amount of variation and the phylogenetic relatedness correlates with the life-history and ecological traits, we did not control for phylogeny in the multivariate models but incorporated the random intercepts of species and study site. We calculated R^2 for the full trait and ecological models using the residual between-study variability (τ^2_{residual}) and the total between-study variability (τ^2_{total}) according to the equation (López-López, Marín-Martínez, Sánchez-Meca, Van den Noortgate, & Viechtbauer, 2014):

$$R^2 = (1 - \tau^2_{\text{residual}} / \tau^2_{\text{total}}) \times 100.$$

3.7 | Publication bias; body mass manipulation

We used funnel plots to visually check for potential asymmetry caused by publication bias in each trait category (Supporting Information Figure S5). To quantify the level of asymmetry in each trait category, we applied the Egger's regression tests of the meta-analytical residuals from all null models of the trait categories (calculated using the *rma.mv* function) against effect size precision (1/mean-adjusted standard error; Nakagawa & Santos, 2012). An intercept significantly differing from zero suggests the presence of publication bias. In order to find differences in log body mass between the tagged and control individuals during the tagging and marking, we applied a linear mixed-effect model with species and study site as a random intercept weighted by the sample sizes. We considered all effect sizes significant when the 95% credible interval (CrI; using *MCMCglmm* function) or confidence interval (CI; using *rma.mv* function) did not overlap zero. All analyses were conducted in R version 3.3.1 (R Core Team, 2018).

4 | RESULTS

We assessed 854 records for eligibility of effect size calculation and excluded 36% of these records mainly due to a missing control group (59% of ineligible records) or missing essential values for effect size calculation (21%; Supporting Information Figure S1). Finally, a total of 122 studies containing 549 effect sizes were included in our meta-analysis wherein 35% effect sizes originated from unpublished sources (Table 2). The vast majority of the analysed effect sizes originated from Europe or North America (94%; Supporting Information Figure S6) and the data contained information about 7,829 tagged and 17,834 control individuals of 69 species from 27 families and 7 orders (Supporting Information Table S7).

We found a weak overall negative effect (Hedges' *g*: −0.2; 95% CrI −0.29, −0.11; $p < 0.001$) only on apparent survival in the model not controlled for phylogeny (model 1). Although we found no statistically significant overall tagging effects in any trait category when controlling for phylogenetic relatedness, the estimates were

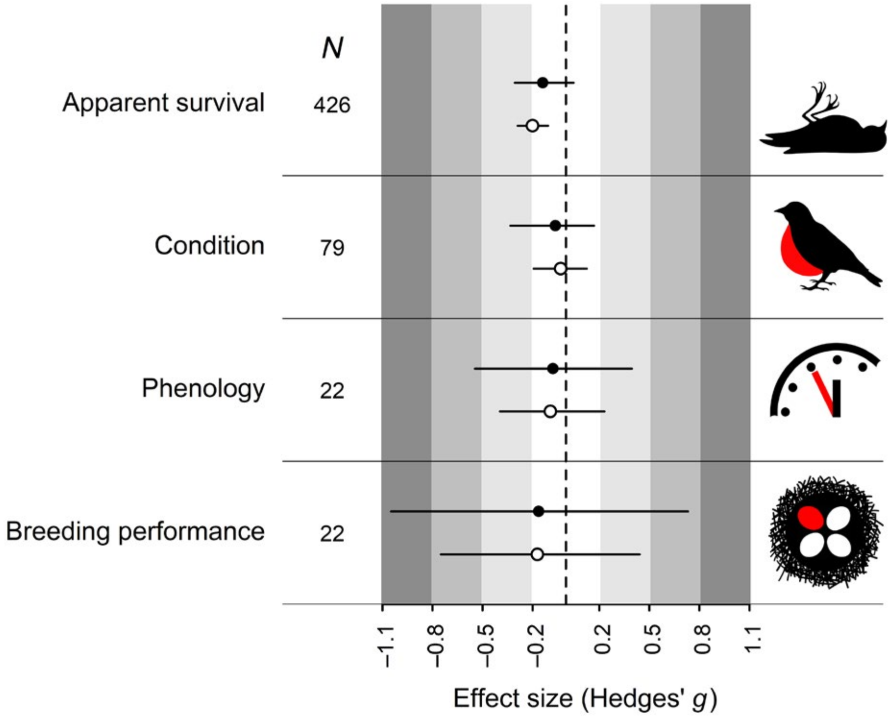

FIGURE 1 Overall effects of geolocators in the four trait categories, circles give means, horizontal lines represent 95% CrI. Filled symbols present the phylogenetically controlled overall effects, open symbols give the value from null models not accounting for phylogeny. *N* presents the number of effect sizes analysed. For the detailed description of the trait categories, see Methods and Supporting Information Table S2

TABLE 3 Summary of the full trait model (n = 281; model 3) and the ecological model (n = 426; model 4) of the geolocator effects on apparent survival. Levels contrasted against the reference level are given in parentheses

Trait	Estimate	*SE*	*Z*	95% CI	*p*
Full trait model					
Intercept	−0.25	0.10	−2.59	(−0.44; −0.06)	0.010
Published (published)	0.14	0.10	1.39	(−0.06; 0.34)	0.164
Control type (matched)	−0.05	0.09	−0.61	(−0.23; 0.12)	0.542
Foraging strategy (aerial)	−0.09	0.14	−0.61	(−0.36; 0.19)	0.540
Sex (males)	−0.07	0.05	−1.30	(−0.17; 0.03)	0.192
Relative load	−0.12	0.05	−2.36	(−0.23; −0.02)	0.018
Stalk/pipe length	0.07	0.04	1.77	(−0.01; 0.15)	0.077
Material elasticity (non-elastic)	0.19	0.08	2.21	(0.03; 0.35)	0.026
Foraging strategy (aerial) × stalk length	−0.10	0.07	−1.40	(−0.25; 0.04)	0.161
Ecological model					
Intercept	−0.26	0.08	−3.20	(−0.42; −0.10)	0.001
PC1	0.06	0.03	2.32	(0.01; 0.11)	0.026
PC2	0.02	0.03	0.47	(−0.05; 0.08)	0.638
Dense habitat (yes)	0.03	0.13	0.21	(−0.22; 0.27)	0.834
Nest type (open)	0.14	0.11	1.27	(−0.08; 0.36)	0.205

similar to those not controlled for phylogeny (model 2, Figure 1). The phylogenetic signal (H^2 = 59%) was statistically significant only for apparent survival, suggesting that closely related species have more similar response to tagging than less related species, but the variances explained by phylogeny and species were very low for all models (Supporting Information Table S8).

The full trait model of apparent survival revealed that tagging effects were stronger with increasing load on tagged individuals and that geolocators with elastic harnesses affected birds more negatively than geolocators with non-elastic harnesses (Table 3, Figure 2). However, we found no statistically significant effect on apparent survival for control group type, sex, stalk length, foraging strategy or the interaction between stalk length and foraging strategy (model 3, Table 3). The ecological model suggested a relationship of apparent survival with the PC1, with negative effects being stronger with decreasing body, egg and clutch mass (model 4, Table 3).

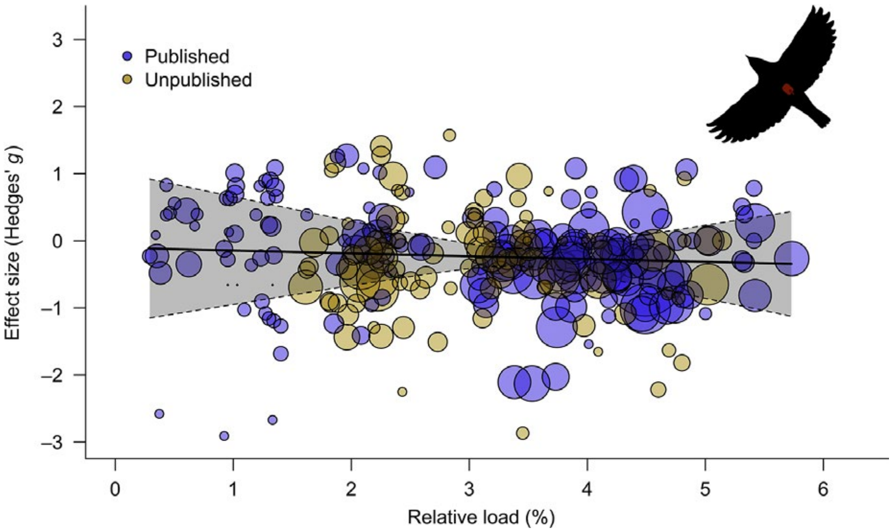

FIGURE 2 Relationship between relative load and the effect of geolocator deployment on the apparent survival of tagged birds. Size of the circles reflects the precision (1/mean-adjusted *SE*) of the effect sizes, the shaded area and dashed lines depict the 95% CI of the regression

The full trait model explained 21.1% and the ecological model 11.8% of the between-study variance.

We did not find any evidence for publication bias in any of the trait categories, either visually in the funnel plots (Supporting Information Figure S5), or using Egger's regression tests (Table 2). Moreover, there were no statistically significant differences in tagging effects between published and unpublished studies (model 5, Supporting Information Table S9). The geolocator-tagged birds were on average 3.8% heavier than control individuals prior to the geolocator deployment and marking (LMM: estimate 0.008 ± 0.003, $t = 2.47$, $p = 0.014$).

5 | DISCUSSION

Geolocator deployment has a potential to reduce a bird's apparent survival, condition, breeding performance or may delay events of the annual cycle leading to biases in movement data. By conducting a quantitative review of published studies deploying geolocators on small bird species and incorporating unpublished data, we revealed only a weak overall effect of geolocators on apparent survival of tagged birds while we found no clear overall effect on condition, phenology and breeding performance. Moreover, we found no statistically significant effects of tagging in any of trait categories when accounting for phylogenetic relationships. Tagging effects on apparent survival were stronger with a higher relative load, when the geolocators were attached with elastic harnesses and in small-bodied species.

5.1 | Overall tag effects

A negative overall effect of geolocator tagging on apparent survival found in this study seems to be prevalent across previous comparative studies of tagging effects (Barron et al., 2010; Bodey et al., 2018a, 2018b; Costantini & Møller, 2013; Trefry, Diamond, & Jesson, 2012; Weiser et al., 2016). However, unlike previous comparative (Barron et al., 2010; Bodey et al., 2018a, 2018b) and primary studies (e.g. Adams et al., 2009; Arlt et al., 2013; Snijders et al., 2017), we found no overall negative effects of tagging on variables associated with breeding performance in our analysis. We also did not find evidence for overall effects of tagging on body condition and phenology, which was consistent with equivocal results of previous studies: Some found reduced body condition (Adams et al., 2009; Elliott et al., 2012) or delayed timing of annual cycle events (Arlt et al., 2013; Scandolara et al., 2014), while others found no evidence for tagging effects on these traits (Bell et al., 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk et al., 2015).

Tagged individuals that returned to the study site are potentially in better condition than the tagged individuals that did not return—this potentially contributes to the weak tagging effects on condition, phenology and breeding performance. However, the lack of effect we found on phenology and breeding performance could also be an artefact of the small sample sizes, as collecting these data is probably more challenging in small avian species, which are more difficult to re-sight and recapture and have shorter life spans than the relatively heavier species included in the previous studies. Similarly, effects of tagging on condition could be underestimated in our analysis due to the initial differences we found between the body mass of tagged and control birds. Additionally, the intra-annual body mass changes could be biased in studies where timing of geolocator deployment and geolocator recovery differs. Unfortunately, the timing of captures and recaptures was rarely reported and could not be analysed in our study. Overall, the weak effects of tagging we found support several primary studies (e.g. Bell et al., 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk et al., 2015), indicating that geolocator tagging is both ethical and provides credible information on bird movements. On the other hand, care should be taken as the tagging effect may be specific to populations or species. For example, Weiser et al. (2016) found a negligible overall effect but significant reduction of return rates in the smallest species in their meta-analysis. The negative effect of geolocators can also vary between years (Bell et al., 2017; Scandolara et al., 2014), or be induced by occasional bad weather conditions (Snijders et al., 2017), or food shortages (Saraux et al., 2011; Wilson, Sala, Gómez-Laich, Ciancio, & Quintana, 2015).

5.2 | Inferring unbiased overall effect sizes

We minimized publication bias in our estimates of overall effects by including substantial amount of unpublished results (192 records of 38 species) and contacting authors of published studies for additional data. Still, some of these studies might get published in the future despite the delay between our data collation and the final analysis. We did not find any evidence that tagging effects differed between published and unpublished studies, suggesting that the tagging effect may not be a critical consideration for publishing a study.

Moreover, we found no support for stronger tag effects in studies with matched control individuals compared to studies with less strict control treatments. However, this result is potentially confounded by the fact that tagged birds were on average larger and in potentially better condition than control birds, which would underestimate the negative effects of tagging. We thus suggest establishing carefully matched control groups in all future studies to enable a more reliable estimation of tagging effects. Such a control group should include the following: (a) randomly selected individuals of the same species, sex and age class; (b) individuals caught at the same time of the season and year; (c) at the same time of the day; (d) of similar size and condition as tagged individuals; and (e) exclude non-territorial birds or individuals passing through the site.

5.3 | Influence of relative load and species' life histories

Our results support the current evidence (Bodey et al., 2018a, 2018b; Weiser et al., 2016) for reduced apparent survival in studies with a relatively higher tag load on treated individuals. Moreover, we found an increasing negative effect in studies tagging smaller species with smaller eggs and clutch masses. The lower body mass in these species is likely accompanied with a higher relative tag load due to technical constraints of lower tag weights. Although recent miniaturization has led to the development of smaller tags, these tags have been predominantly applied to smaller species instead of reducing tag load in larger species (Portugal & White, 2018). The various relative loads used without observed tagging effects (e.g. Bell et al., 2017; Peterson et al., 2015; van Wijk et al., 2015) indicate the absence of a generally applicable rule for all small bird species (Schacter & Jones, 2017), and we thus recommend the use of reasonably small tags despite potential disadvantages (e.g. reduced battery life span or light sensor quality).

5.4 | Harness material

Contrary to our prediction, we found higher apparent survival in birds tagged with harnesses made of non-elastic materials. Non-elastic harnesses are usually individually adjusted on each individual, whereas elastic harnesses are often prepared before attachment to fit the expected body size of the tagged individuals according to allometric equations (e.g. Naef-Daenzer, 2007). As pre-sized elastic harnesses cannot match perfectly the size of every captured individual, they may be in the end more frequently tightly fitted as some researches might tend to tag larger individuals or avoid too loose harnesses to prevent geolocator loss. Non-elastic harnesses may also be more frequently looser than elastic harnesses as researchers try to reduce the possibility of non-elastic harness getting tight when birds accumulate fat. Tight harnesses significantly reduced the return rates in whinchat (*Saxicola rubetra*; Blackburn et al., 2016), and it may be difficult to register whether elastic harnesses are restricting physical movement of birds when deploying tags. In contrast, non-elastic harnesses, which are more commonly tailored according to the actual size, are often made sufficiently loose to account for body mass changes in each individual. Prepared elastic harnesses are usually used to reduce the handling time during the geolocator deployment (Streby et al., 2015) but this advantage may be outweighed by the reduced apparent survival of geolocators with tied elastic harnesses. We thus suggest to consider stress during geolocator deployment together with the potentially reduced apparent survival and the risk of tag loss when choosing harness material.

5.5 | Variables without statistically significant impact on tagging effect

Migratory distance did not affect the magnitude of the effect sizes, contrasting with some previous findings (Bodey et al., 2018a, 2018b; Costantini & Møller, 2013). However, none of these studies used population-specific distances travelled; instead, they used latitudinal spans between ranges of occurrence (Costantini & Møller, 2013) or travelled distance categorized into three distances groups (Bodey et al., 2018a, 2018b). These types of distance measurements could greatly affect the results especially in species that migrate mainly in an east–west direction (Lislevand et al., 2015; Stach, Kullberg, Jakobsson, Ström, & Fransson, 2016) or in species whose populations largely differ in their travel distances (Bairlein et al., 2012; Schmaljohann, Buchmann, Fox, & Bairlein, 2012). Moreover, light-level geolocators were most frequently deployed to the long-distance migrants in our study and the result can be thus applicable to these species only.

Additionally, we found no overall effect of species' foraging strategy, contrary to the strong overall negative effect found for aerial foraging species (Costantini & Møller, 2013). Despite the tag shape altering the drag and thus energy expenditure during flight (Bowlin et al., 2010; Pennycuick et al., 2012), apparent survival tended to be better in individuals fitted with stalked geolocators and we found no interaction between stalk length and foraging strategy on the tagging effect size. Geolocators with longer stalks have been more frequently used in heavier birds with low relative load where the expected tag effect is weak. Moreover, previous results of strong negative effects in aerial foragers led to a preferential use of stalkless geolocators in these species and probably minimized the tagging effect in this foraging guild (Morganti et al., 2018; Scandolara et al., 2014). However, the evidence for the negative effects in non-aerial foragers is low as there is only one field study focusing on stalk length effects on the return rates (Blackburn et al., 2016).

5.6 | Future considerations

Future studies evaluating the use of geolocators on birds should focus on assessing interannual differences in tagging effects, effects of varying relative loads, different stalk lengths or different attachment methods to minimize the negative effects of tagging. We also suggest to focus on the impact of various movement strategies such as fattening and moulting schedules on the tagging effect. All future studies should carefully set matched controls and transparently report on tagging effects. Finally, our results encourage use of geolocators on small bird species but the ethical and scientific benefits should always be considered.

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AUTHORS' CONTRIBUTIONS

V.Br., J.K. and P.P. conceived the idea and designed the methodology. V.Br. reviewed the literature and collected data. J.K. and P.P. checked the data extracted for analysis. V.Br. and P.P. analysed the data. V.Br. led the writing of the manuscript with significant contributions from J.K. and P.P. M.B., S.H., D.H., M.K., J.O. and E.W. contributed with unpublished data and their comments and suggestions significantly improved the manuscript. P.A., J.A., D.A., S.B., D.B., E.B., V.Be., C.B., S.B., M.Br., B.C., D.C., N.C., J.C., V.C., T.E., K.F., O.G., M.G., M.H., C.H., F.J., J.J., T.K., D.K., M.L., T.L., S.L., C.L., K.M., P.Mar., S.M., P.Mat., C.M., B.M., J.M., R.Ne., A.N., R.No., T.P., V.P., N.P., M.P., J.R., C.R., A.R., C.S., N.S., M.T., D.T., H.O., A.W., H.W., J.W., K.W. and B.W. contributed unpublished data and critically revised the manuscript. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data described in this article are available at https://doi.org/10.5281/zenodo.1886530 (Brlík et al., 2019).

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SUPPORTING INFORMATION

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